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CHANGING NEST PLACEMENT OF HAWAIIAN COMMON AMAKIHI DURING THE BREEDING CYCLE

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ABSTRACT.—We studied the nesting behavior of the Common Amakihi (*Hemignathus virens*) from 1970–1981 on the island of Hawaii to determine if the species alters nest placement over a protracted 9-month breeding season. Birds preferentially chose the southwest quadrant of trees in which to build nests during all phases of the breeding season. It appeared that ambient temperature (Ta) was a contributing factor to differential nest placement between early and late phases of the annual breeding cycle. When Ta is low during the early (December–March) breeding period, Common Amakihi selected exposed nesting locations that benefitted them with maximum solar insolation. However, in the later phase of the breeding period (April–July) when Ta was much higher, renesting birds selected nest sites deeper in the canopy in significantly taller trees. This is one of the few documented examples in which a species changes location of nest during a breeding season, thus allowing exploitation of temporally differing microclimatic conditions. *Received 24 Aug. 1992, accepted 21 Jan. 1993.*

The Common Amakihi (*Hemignathus virens*) is a small (ca 12–15 g) passerine of the endemic Hawaiian Drepanidinae. It presently occurs on five of the six major Hawaiian islands and is the second most abundant native land bird in the archipelago (Scott et al. 1986). We studied the species between 1600 and 2600 m elevation on the southwestern slope of Mauna Kea volcano, on the island of Hawaii (Fig. 1). This forest is one of the highest nesting locations of the Common Amakihi in Hawaii (Berger 1981).

Baldwin (1953), Berger (1969), Kern and van Riper (1984), and van Riper (1976, 1977, 1984, 1987) have documented aspects of Common Amakihi breeding behavior on Hawaii, while Eddinger (1970) did the same on Kauai. The species nests from near sea level to tree line which, on the larger islands, spans 3000 m elevation. Although most nesting occurs from March through May, active nests have been found from November through August. A typical breeding season begins in December, with first nests active until March; a second breeding phase begins in April and usually lasts through July. The birds are monogamous and retain the same mate for successive breeding seasons. Nests are statant, and during

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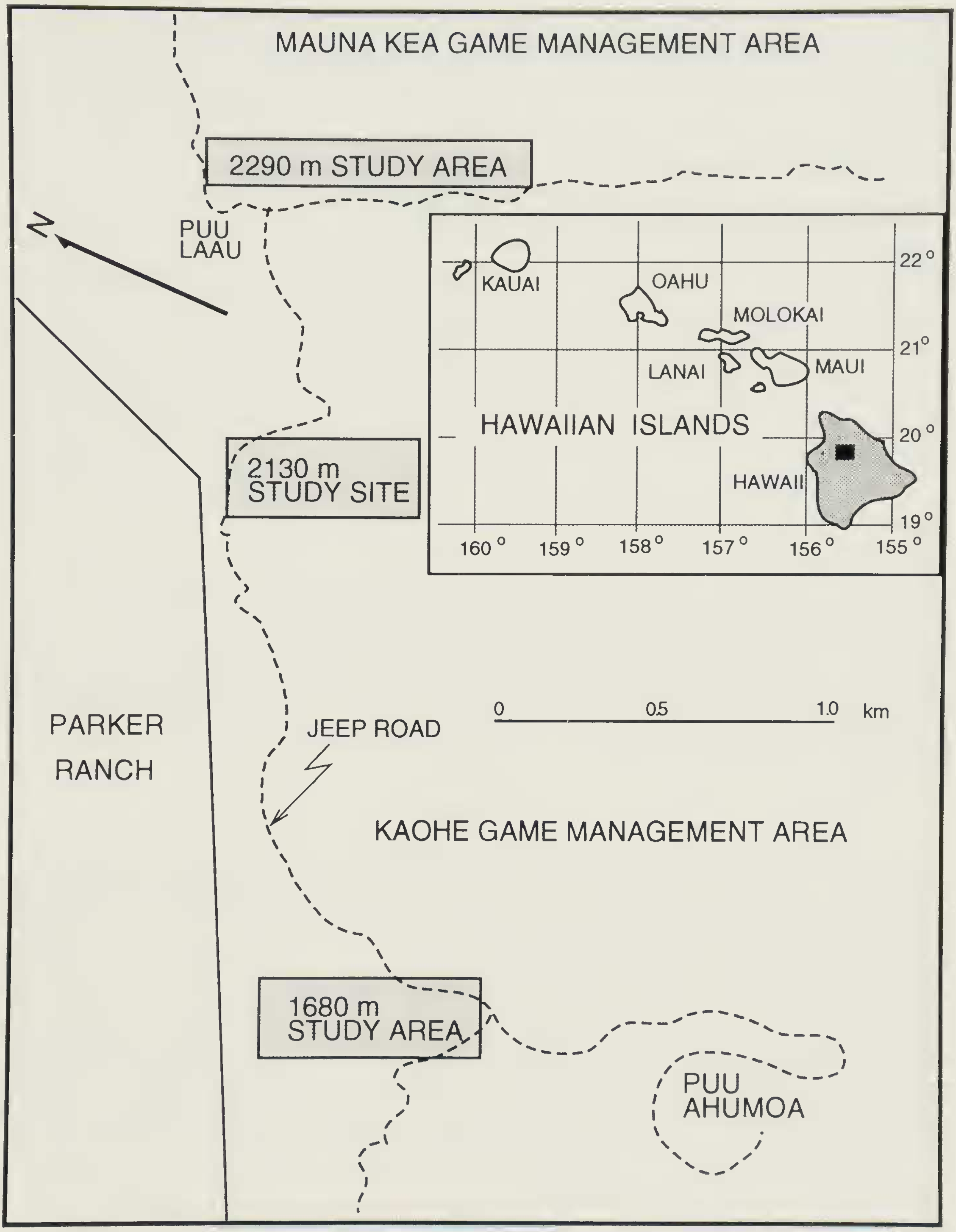

FIG. 1. Map of the study area on the southwestern slope of Mauna Kea, Hawaii.

the 9-month breeding cycle, a pair may successfully raise two broods of young (van Riper 1987).

The study area essentially is a savannah with widely-spaced trees and intervening areas covered by introduced grasses and a few shrubs. The two dominant tree species, mamane (*Sophora chrysophylla*) and naio (*Myoporum sandwichensis*), are evergreens and the principal species that Common Amakihi use for nesting (van Riper 1987). The climatic conditions of the area are extreme and variable. It is in Mauna Kea's rain shadow and, consequently, quite dry (Price 1966). The high elevation also subjects birds to extremes in temperature. Nocturnal temperatures frequently fall below freezing during the early months of the breeding season. Daytime temperatures are much warmer during the late part of the breeding cycle (van Riper 1980). As a result, abiotic factors that influence breeding are more variable than for species with restricted breeding seasons. Moreover, the many different elevations and habitats in which this species breeds suggest that it is able to adjust its breeding behavior to diverse situations.

To determine if Common Amakihi used different nesting locations in the early (December–March) and late (April–July) phases of the breeding season and if this change was microclimatically adaptive, we studied a population on the southwestern slope of Mauna Kea, Hawaii. We hypothesized that the Common Amakihi, because of its small size and protracted breeding season, would exhibit temporal variations in nest placement, building early nests in the warmer southern hemisphere of a tree while later nests would be constructed in the cooler, northern side of the canopy.

METHODS

From 1970 through 1981 we studied Common Amakihi nesting behavior. Birds were captured in mist nets and marked with unique combinations of colored plastic leg bands and a single U.S. Fish and Wildlife Service metal band. During 1970–1975, the following information was recorded at nest sites: location of the nest within the study area; nest height (distance from ground to the bottom of the nest); nest-tree height and species; circumference of nest-tree at breast height (1.4 m from the ground); distance from nest to axis of trunk and distance to end of branch; nest azimuth (with a compass) from center of trunk; and nest placement within the tree. During the 1974 and 1975 breeding seasons, nests were located during construction and followed through the fledgling period. We compared success among these nests on the basis of young fledged vs no young fledged, number of young fledged per nest, and productivity (number of eggs laid that fledged young), relating these to each of six nest placement variables.

From 1970 through 1975, temperature extremes were recorded daily at 2230 m elevation with two unshielded maximum-minimum thermometers, one under a tree canopy and one in the open. Humidity and temperature measurements were recorded continuously with a hygrothermograph. Data obtained from the National Weather Service rain gauge located in our study area were used as a measure of monthly precipitation. Percent cloud cover was recorded throughout the day in the field, with notations made whenever there was a greater than 25% (±10%) cloud cover change during the day. Wind direction and speed (using the Beaufort Scale) were recorded on a daily basis and time noted whenever a one-step change of the latter occurred. This was supplemented with wind speed and direction data from Bradford Air Force Base 4 km from the study area.

Nest placement data from 1970 to 1974 were analyzed to determine the most common nesting location in mamane. During 1975, in a mamane tree that had been utilized previously for nesting, Yellow Spring Instrument Co. shielded thermocouples were placed in lateral forks and on branches representing typical nest sites on the north and south sides of the tree. We chose north and south exposures to test potential microclimatic temperature differences between sides of the tree that receive minimum and maximum solar radiation. Temperature was monitored with Rustrak recorders simultaneously on both sides of the tree for a minimum of three 24-h periods during the early and late periods of the breeding cycle.

To avoid violating assumptions of independence within a day, we analyzed only data points recorded every fourth hour (04:00, 08:00, 12:00, 16:00, 20:00, and 24:00 h HST) for continuously recorded weather and temperature probe data. Weather, nest location parameters (except azimuth), and productivity data were analyzed with student's t-test or ANOVA/PROC GLM (SAS PC 5.0). Percent cloud cover was arcsine transformed prior to analysis. Canopy temperature data were compared using paired t-tests. Nest azimuth data were examined with the Rayleigh test for circular statistics (Batschelet 1981). Statistical significance was accepted when $P < 0.05$.

RESULTS

Nest location.—During this study, 228 nests were measured for at least one of the six placement variables (Table 1). There was no significant difference in nest azimuth between early (December–March; N = 96 nests) and late (April–July; N = 107 nests) phases of the breeding season. Nests were more common in the SW quadrant of both mamane and naio trees ($\bar{\phi} = 210°$; $r = 0.22$; $P < 0.001$), regardless of time in the breeding season (Fig. 2), with this trend stronger in 1974 than in 1975.

We found virtually no difference between early and late season nest height, distance of the nest to the tree center, or circumference at breast height of the nest-tree (Table 1). Only nest-tree height and distance of nest to end of branch varied significantly between early and late breeding periods. Therefore, Common Amakihi utilized significantly taller trees in which to nest late in the breeding season. Since tree size is not significantly different within an elevation stratum on Mauna Kea (van Riper 1980), it appears that birds are selecting specific (larger) trees within their territories in which to renest, thus enabling them to locate their nest farther in from the end of the branch while still keeping it shaded by the canopy.

Productivity.—Success of various nesting locations was analyzed for 111 Common Amakihi nests for which complete data were available for 1974 and 1975. We found that during 1974 successful nests were placed significantly different from random, with directional selection for the SW quadrant (Rayleigh test; $\bar{\phi} = 275°$; $r = 0.29$; $P < 0.05$). There were no other significant productivity differences, between years or within combined years, as a function of the six nest placement variables.

Common Amakihi are long-lived for a small passerine and, as a result, turnover within a breeding population is quite low (van Riper 1987).

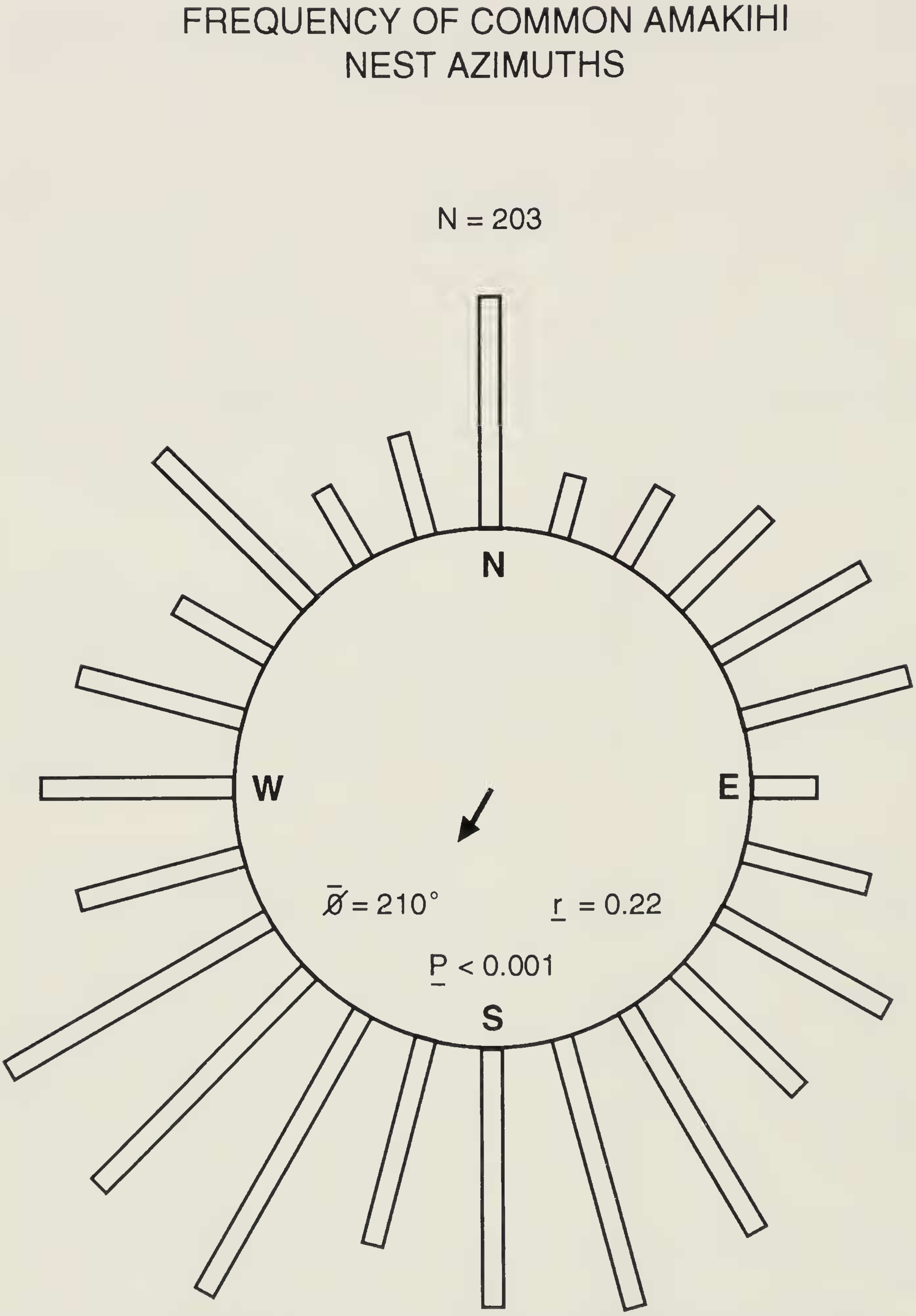

FIG. 2. Locations of Common Amakihi nests in nest trees. Length of open bars indicate number of nests at each azimuth. This figure is based on a sample of 203 nests collected from 1970 to 1975 on the southwestern slope of Mauna Kea, Hawaii. $\bar{\phi}$ = mean angle of sample; r = length of mean vector (angle).

TABLE 1

PHYSICAL ASPECTS OF COMMON AMAKIHI NEST PLACEMENT BETWEEN EARLY AND LATE BREEDING SEASONS

Variable	Early season	Late season	Significance
Tree height (m)	6.2 ± 1.5 (102)	6.8 ± 1.4 (115)	$P < 0.01$[a]
Circumference at breast height (cm)	62 ± 36 (101)	65 ± 35 (114)	$P = 0.73$[a]
Nest height (m)	4.6 ± 1.1 (101)	4.6 ± 1.2 (127)	$P = 0.83$[a]
Distance to center of tree (m)	2.6 ± 1.4 (97)	2.6 ± 1.6 (114)	$P = 0.90$[a]
Distance to end of branch (cm)	5.9 ± 5.4 (49)	8.4 ± 5.8 (114)	$P < 0.01$[a]
Nest azimuth (degrees)	193° (96) $r = 0.18$	217° (107) $r = 0.26$	$P > 0.05$[b]

[a] = Student's t-test.

[b] = Rayleigh test.

[c] Values given are the means ± one SD, with sample sizes in parentheses.

Although we found only 13 pairs of first-time breeders during our study, we attempted to analyze if their nest placement was consistent with those of the more experienced breeders, and if there were differences in productivity of their nesting locations. We found no significant difference in any aspect of nest placement, clutch size, or productivity between first-time and older breeders (Table 2).

Climate.—The daily weather pattern on the upper southwestern slope of Mauna Kea is characterized by clear mornings, with clouds forming in the early afternoon as the inversion layer breaks down and up slope movement of warmer air and associated cloud cover occurs. We found no significant difference in percent monthly cloud cover over the annual cycle ($P > 0.05$; Fig. 3). The constant trade winds characteristic of Hawaii (Price 1966) were not common in the study area because of orographic constraints imposed by Mauna Kea. Winds were generally from the southwest, the result of up-slope movement of air due to surface heating. Strong winds (≥ 6 on the Beaufort Scale; ≥ 40 km/h) occurred infrequently. In 1974 only six of 240 days had winds greater than six, and only one of 180 days during 1975 had wind speeds of this magnitude.

Water vapor pressure (mm Hg), calculated from temperature and humidity data, differed significantly between early and late breeding seasons during our study (Table 3). Water vapor pressure increased significantly in the later part of the breeding season due to the influence of warmer daily temperatures.

Annual precipitation at Puu Laau averaged 51.1 ± 18.3 cm from 1932

TABLE 2

A COMPARISON OF RETURNING AND FIRST-TIME BREEDING COMMON AMAKIHI NEST PLACEMENT AND PRODUCTIVITY VARIABLES DURING 1973–1975 ON THE SOUTHWESTERN SLOPE OF MAUNA KEA, HAWAII (SEE TEXT FOR EXPLANATION OF VARIABLES)

Variable	Returning breeders	First-time breeders	Significance
Tree height (m)	6.8 ± 1.3 (24)	6.6 ± 0.9 (13)	$P = 0.58^a$
Circumference at breast height (cm)	64 ± 32 (24)	51 ± 21 (13)	$P = 0.20^a$
Nest height (m)	4.9 ± 0.9 (24)	5.0 ± 1.0 (13)	$P = 0.85^a$
Distance to center of tree (m)	3.0 ± 1.7 (24)	3.1 ± 1.5 (13)	$P = 0.85^a$
Distance to end of branch (cm)	10.2 ± 7.2 (24)	6.6 ± 5.8 (12)	$P = 0.14^a$
Nest azimuth (degrees)	215° (24) $r = 0.12$	86° (13) $r = 0.20$	$P > 0.90^b$
Clutch size	2.3 ± 0.6 (20)	2.3 ± 0.5 (7)	$P = 0.95^a$
Productivity	6.3 ± 3.0 (18)	5.8 ± 4.0 (8)	$P = 0.75^a$

[a] = Student's *t*-test.

[b] = Rayleigh test.

[c] Values given are the means ± one SD, with sample sizes in parentheses. Nest azimuth is expressed as the mean angle (vector) of the sample, relative to the center of the tree.

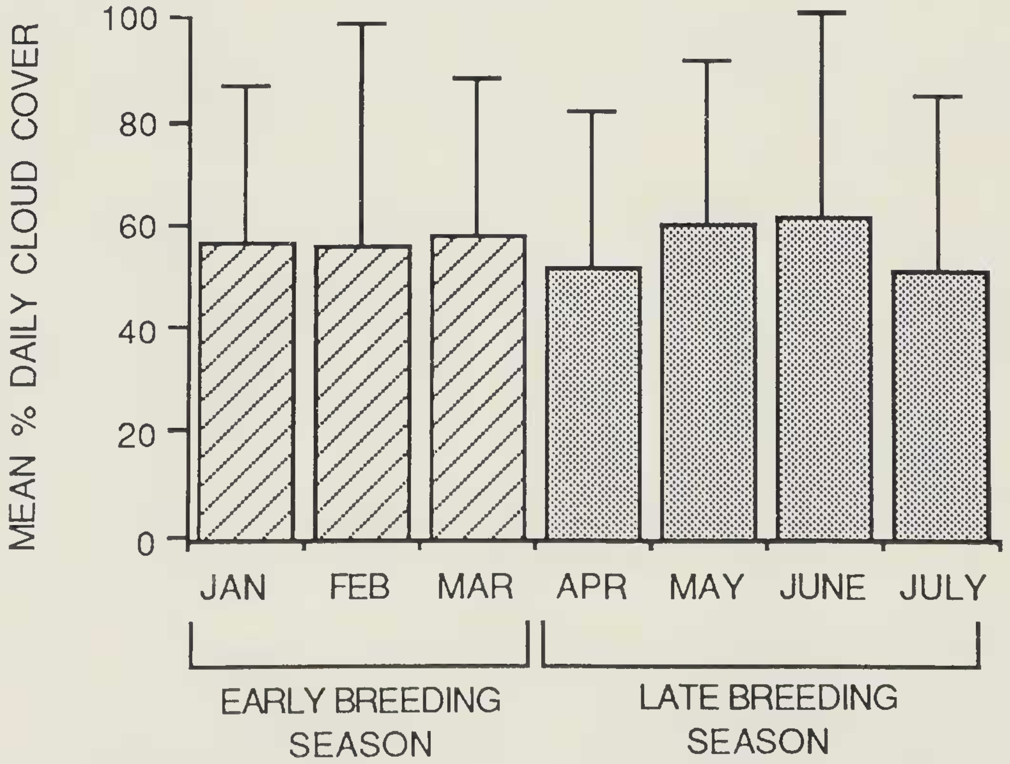

FIG. 3. Cloud cover patterns during the 1973–1975 Common Amakihi breeding seasons at 2130 m elevation on the southwestern slope of Mauna Kea, Hawaii. Vertical lines are ± one SD.

TABLE 3

RELATIVE HUMIDITY, AVERAGE TEMPERATURES, WATER VAPOR PRESSURE (MM HG), AND RAINFALL RECORDED DURING 1973–1975 AT 2130 M ELEVATION ON THE SOUTHWESTERN SLOPE OF MAUNA KEA, HAWAII

Variable[a]	December–March	April–July	Significance
Relative humidity (%)	73 ± 16 (60)	59 ± 16 (89)	$P < 0.0001$
Temperature (°C)			
Mornings	11.0 ± 3.6 (60)	13.0 ± 2.7 (90)	$P < 0.005$
Daily	9.1 ± 2.5 (60)	10.4 ± 2.2 (90)	$P < 0.002$
Ambient vapor pressure (mm Hg)	6.5 ± 1.2 (58)	9.6 ± 1.8 (89)	$P < 0.0001$
Rainfall (cm)	4.6 ± 4.2 (12)	2.2 ± 2.4 (12)	$P > 0.05$

[a] Numbers are means ± one SD with sample sizes in parentheses. Comparisons were made using Student's *t*-test.

through 1972, with monthly rainfall during the early Common Amakihi breeding period (December–March) averaging 5.9 ± 4.4 cm and the late breeding period (April–July) averaging 4.0 ± 4.2 cm (van Riper 1980). The years of 1973–1975 experienced typical rainfall, with only three months falling outside expected precipitation ranges, although the late breeding period was somewhat drier than the prior 40 year average (Table 3).

Because of the high elevation, day and night temperatures fluctuated over a 20°C range. Although mean nighttime temperature did not differ significantly between early and late breeding season ($t = -0.97$; $P = 0.33$), mean daytime temperatures were significantly higher during the latter half of the breeding season ($t = -3.62$; $P < 0.01$; Table 3). Temperature extremes from max-min thermometers placed inside and outside the canopy revealed that temperatures outside fluctuated more than inside the canopy (Fig. 4). There was a significant difference between high temperatures (*t*-test; $P < 0.05$) but not low temperatures. However, a nocturnal canopy buffering effect was evident in that low temperatures were slightly warmer throughout the night inside the canopy. Rustrak temperature recorder data from "typical" nest sites showed that during the early nesting period (temperatures recorded 18–21 February), there was no significant difference in temperature between the north and south lateral forks. However, during the later breeding period (temperatures recorded 10–12 April), the south side lateral forks were significantly warmer ($t = -19.8$; $P < 0.01$).

DISCUSSION

Throughout evolutionary time, nest site selection has been important in maximizing productivity (Ricklefs 1969). For example, nest placement

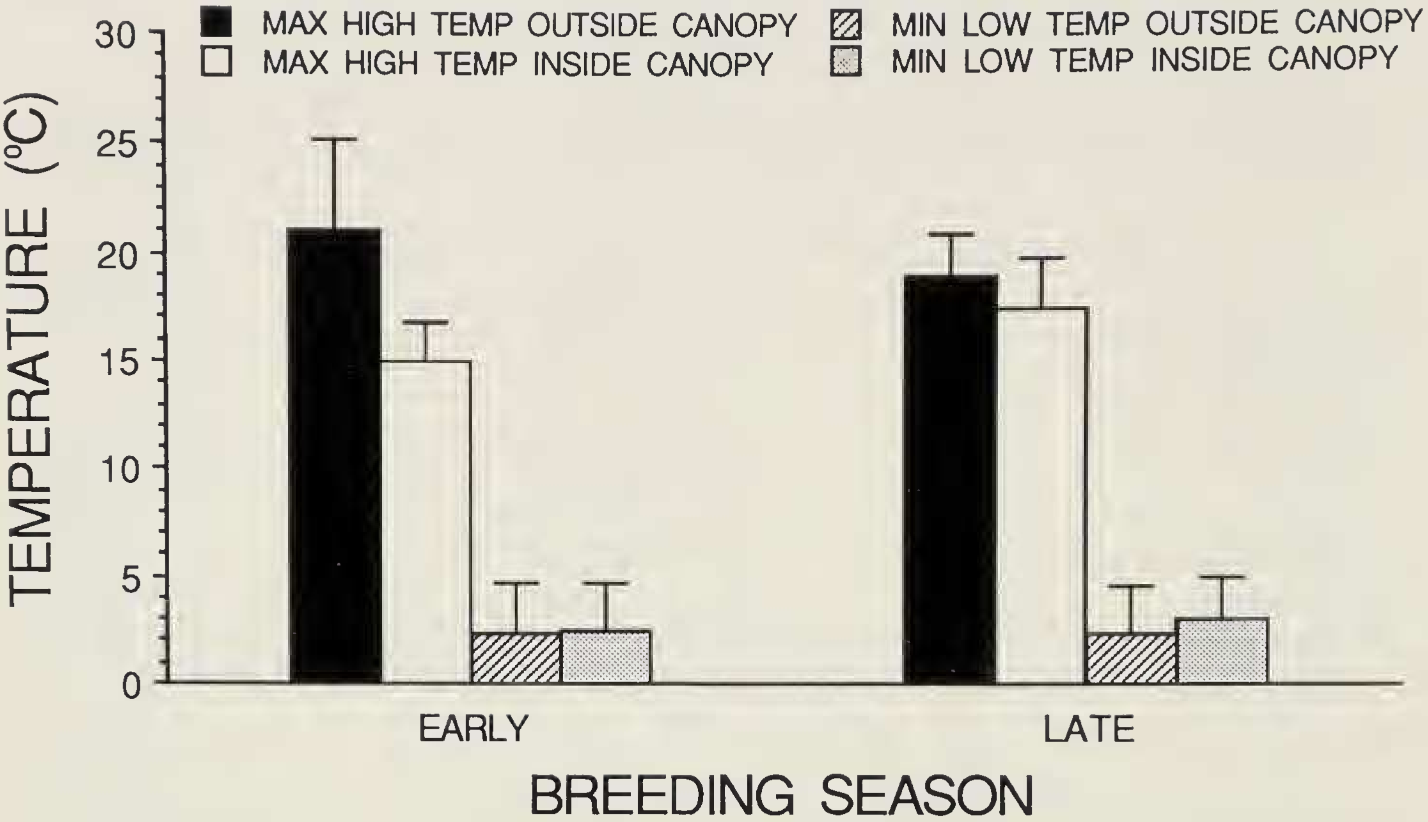

FIG. 4. Temperature extremes inside and outside a nest tree canopy during early (December–March) and late (April–July) parts of the Common Amakihi breeding season. Temperatures were recorded on unshielded high-low thermometers from 1973 to 1975 at 2130 m elevation on the southwestern slope of Mauna Kea, Hawaii. Vertical lines are ± one SD.

potentially affects the number of young fledged and, therefore, ultimately fitness through differential exposure to predators and to abiotic factors such as wind, rain, temperature, and humidity. Many details of the interplay between these factors and resulting behavioral responses of nest placement are still not well understood.

Several studies have shown that birds which construct statant nests alter their nest placement throughout the breeding season (Nice 1937, Horvath 1964, Taylor 1965, Holcomb and Twiest 1968, Holcomb 1969). However, except for hummingbirds, seasonal alterations of nest location have been attributed to factors such as changes in available nesting substrates or an attempt to avoid predation, rather than selection for changed microclimatic conditions.

Horvath (1964) listed three ways in which nesting birds can respond behaviorally to climatic extremes: (1) select appropriate microclimates in which to nest; (2) adapt the nest structure to prevailing climatic factors; and, (3) use behaviors such as brooding and sun shading to protect eggs and/or chicks during microclimatic emergencies. In regard to Horvath's suggestions, (2) and (3) have been documented in the Common Amakihi. Kern and van Riper (1984) showed that this species tailors its nest structure commensurate with prevailing climatic conditions in different habitats on the Hawaiian islands. Van Riper (1987) recorded behaviors such as sun shading and brooding that are exhibited during brief microclimatic extremes. The one behavioral adaptation remaining to be examined is the possibility that Common Amakihi select differing microclimates in which to build nests.

If microclimate is of importance in Common Amakihi nest site selection, it would be expected that nests established during early breeding would be differently located in comparison to those built later in the nesting cycle when climatic factors differ. Our initial hypothesis was that birds would place their early nests in the southern hemisphere, while later nests would be located in the northern hemisphere of the tree. This was not the case. Instead, birds preferentially placed their nests toward the SW quadrant of the nest tree throughout the breeding season, but placed later nests farther into the canopy during the later (and warmer) part of the breeding period.

The overall preferential placement of nests in the southwestern quadrant of the nest tree throughout the entire breeding period may have been due to a number of environmental factors such as exposure to rainfall, prevailing winds, cloud cover, or the need for solar heat for metabolic maintenance and incubation.

Rainfall would not appear to influence greatly nest-site selection because it should affect all sides of the tree equally. Moreover, during 1973–1975 rainfall was consistent with the general precipitation pattern over the previous 40 years. Wind direction may be important, but because the study area is located in the mountain lee, potentially damaging winds occur at infrequent and irregular intervals. There was no significant difference in cloud cover over the annual cycle (Fig. 3); therefore, early and late breeding season nest placement would be influenced in a like manner by this abiotic factor. However, the cooling effect of cloud cover may have influenced nest location throughout the year by favoring placement in the warmer SW quadrant of the nest tree.

It does appear that heat absorption and retention play a major role in determining the location of Common Amakihi nests during the early breeding season. The metabolic saving to a female which nests in a part of the tree having a slightly warmer temperature may be considerable when ambient temperature (Ta) is low, which is the case during the early breeding period (see Table 3). Our nest site probe data showed that temperatures were warmer on the southern tree exposure.

Heat avoidance appears to be important during the day in the second half of the breeding season, because Common Amakihi locate nests in a more sheltered location within the nest tree. MacMillen (1974) found that Common Amakihi do not tolerate high Ta and are unable to control body temperature (Tb) below lethal levels even at only moderately high

Ta. This is undoubtedly accentuated for young that are not able to thermoregulate until day eight of the nestling period. Van Riper (1987) also found that, in those few nests that were exposed to direct sunlight, extensive sun shading by the female occurred during the warmer portions of the day. Therefore, warming of nests, particularly in the morning, may be important for nesting success early in the breeding period, whereas nest cooling during the heat of the day may be important later in the breeding season.

Numerous reports document cases in which birds place their nests at specific locations to take advantage of factors such as solar radiation, wind, and rain (e.g., Rich 1980, Zerba and Morton 1983, Collias and Collias 1984, Kern and van Riper 1984, Bekoff et al. 1987). But our study of Common Amakihi is one of only a few studies (e.g., Horvath 1964, Walsberg 1977) in which a species actually alters location of its nesting during the breeding season. The situation is similar to that of Cactus Wrens (*Campylorhynchus brunneicapillus,* Ricklefs and Hainsworth 1969) and Verdins (*Auriparus flaviceps,* Austin 1976) which do not move the nest, but change the location of the nest entrance between early and late phases of the breeding season.

We believe that the major contributing factor in determining Common Amakihi nest placement on Mauna Kea appears to be the influence of ambient temperature. Low Tas during the early breeding season have selected for nesting locations on the most exposed branches in the southern portion of the nest tree so that the nest benefits from maximum solar insolation. However, later in the breeding season when Tas are much higher, renesting birds select significantly taller trees that have suitable nesting sites farther into the canopy and that offer more microclimatically suitable nesting locations.

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